Stable Fly Population Dynamics in Eastern Nebraska in Relation to Climatic Variables

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ABSTRACT Stable flies, *Stomoxys calcitrans* (L.), are among the most economically important arthropod pests of livestock in North America. In this study, we monitored the seasonal dynamics of a stable fly population in eastern Nebraska for 5 yr. Models based upon temperature and precipitation were developed to determine the affects of these variables on population levels as well as to project population trends. Stable flies appear in eastern Nebraska in late March to early April, and they build to a peak population during the last week of June and first week of July. In most years, the population decreases in midsummer, and then it increases to a second peak in mid-September. Temperature 0 to 2 wk before collection and precipitation 3 to 6 wk before collection were the most important weather variables accounting for 63 and 11% of the variation, respectively. Temperature 7 wk before collection was also significant, accounting for 3% of the variation. Reduced precipitation levels explained the observed midsummer drop in the stable fly populations. Changes in stable fly population levels were positively correlated with precipitation 1 to 2 wk prior and temperature the week of the change. Population change was negatively correlated with precipitation 6–8 wk prior and temperature 6–15 wk prior. The addition of the previous weeks trap collections to the climate based model eliminated the significance of temperature 2 and 7 wk before collection. Temperature 0–1 wk before collection accounted for 60% of the variation, precipitation 3 to 6 wk prior 12% of the variation, and the previous weeks' trap collections accounted for 11% of the variation. Low temperatures during October through January were correlated with higher stable fly populations the following June and July.

KEY WORDS *Stomoxys*, climate, population model

Stable flies are among the most important arthropod pests of livestock with damage estimated to exceed $1 billion per year in the United States (Taylor and Berkebile 2006). In spite of their economic impact, the dynamics of stable fly populations are poorly understood, especially in pastures where stable flies have become recognized as a major problem within the past 20 yr (Hall et al. 1982, Campbell et al. 2001, Broce et al. 2005). Previous studies have found that stable fly populations in Iowa (Black and Krafsur 1985), eastern Nebraska (Scholl 1986), and eastern Kansas (Broce et al. 2005) typically peak in mid-June and again in mid- to late August.

Factors affecting seasonal population trends and year-to-year variation in stable fly population levels are not well understood, although several studies have indicated wetter or cooler than normal weather as being conducive to higher population levels (Scholl 1986, Guo et al. 1998). Attempts to correlate population levels with weather variables have been limited. Broce et al. (2005) found early summer stable fly population levels to be negatively correlated with minimum temperatures from the previous December, January, and February but could find no relationship between population levels and temperature or rainfall during the preceding March, April, or May. Scholl et al. (1985) found no correlation between number of stable flies collected on traps and maximum, minimum, or mean temperature, precipitation, maximum or mean wind speed, humidity, or percentage of cloud cover. Peak season, late April through mid-June, stable fly populations in California were correlated with precipitation the previous March (Mullens and Peterson 2005).

The purpose of this study was to develop climate-based models to identify the effects of weather variables on seasonal patterns in stable fly populations and to predict stable fly population trends. Such models will allow producers to implement control procedures before stable fly populations reach economic injury levels.

Materials and Methods

A stable fly seasonal survey based upon adult trapping was conducted at the University of Nebraska, Agricultural Research and Development Center (ARDC), located near Ithaca, NE. ARDC encompasses ≈4,000 ha of cropland and pasture. A dairy and

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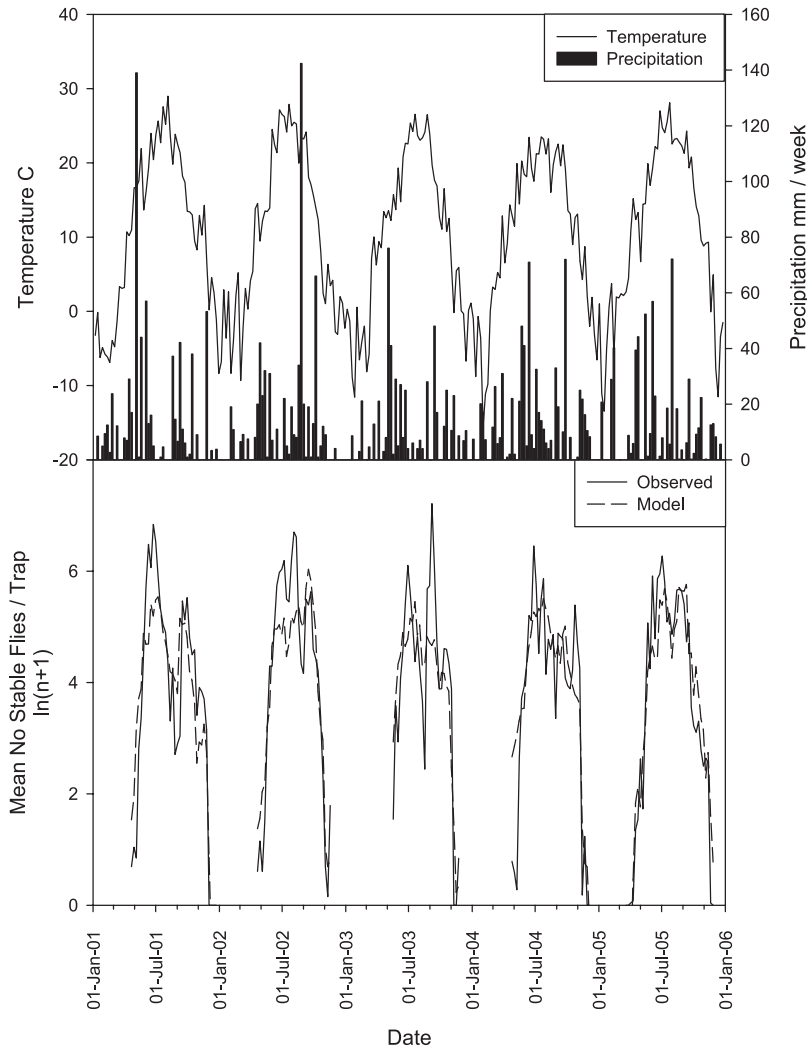[3] Retired; USDA–ARS.

Fig. 1. Temperature and precipitation recorded MEADTURFFARM weather station located on the University of Nebraska Agriculture and Research Development Center, Ithaca, NE (top) and observed and predicted numbers of stable flies per trap from April 2001 to November 2005 (bottom). Temperature is weekly mean of daily averages. Precipitation is weekly total.

feedlot also are located on the property. A large private feedlot (39,000 head) borders the facility to the north. Approximately one-third of the ARDC property is designated pastureland. Broce (1988) Alsynite traps implemented as described by Taylor and Berkebile (2006) were used for this study. In 2001 and 2002, six traps were placed in proximity to several habitats, including feedlot, dairy, composting area, pasture, and cropland. In 2003–2005, 25 traps were placed in a 5- by 5-grid with traps separated by 1 mile (1.6 × 1.6 km). Only one of the six trap locations used for 2001 and 2002 was included in the 25 trap locations used for 2003–2005. Traps were maintained 16 April–18 December 2001, 15 April–14 November 2002, 12 May–20 November 2003, 19 April–22 November 2004, and 14 March–21 November 2005. Traps were collected twice per week (3- or 4-d intervals) throughout most of the season. When fly numbers were low in early and late

season (April through mid-May and October through December, respectively) traps were collected once per week. Dates indicated represent the end of the weekly trapping periods. For comparisons of 2001–2002 data with six traps and 2003–2005 data with 25 traps, all analyses were done with the average number of flies collected per trap.

For comparisons of seasonal data between years, all data are given as weekly totals. Weeks were numbered 1–52 for each year. Week 1 began on 1 January 2001, 31 December 2001, 30 December 2002, 29 December 2003, and 27 December 2004, respectively. Monthly data are averages of 4-wk intervals beginning with week 1 and do not correlate exactly with Julian months.

Climatic data were obtained from the High Plains Regional Climate Center (University of Nebraska, Lincoln, NE) MEADTURFFARM station that is lo-
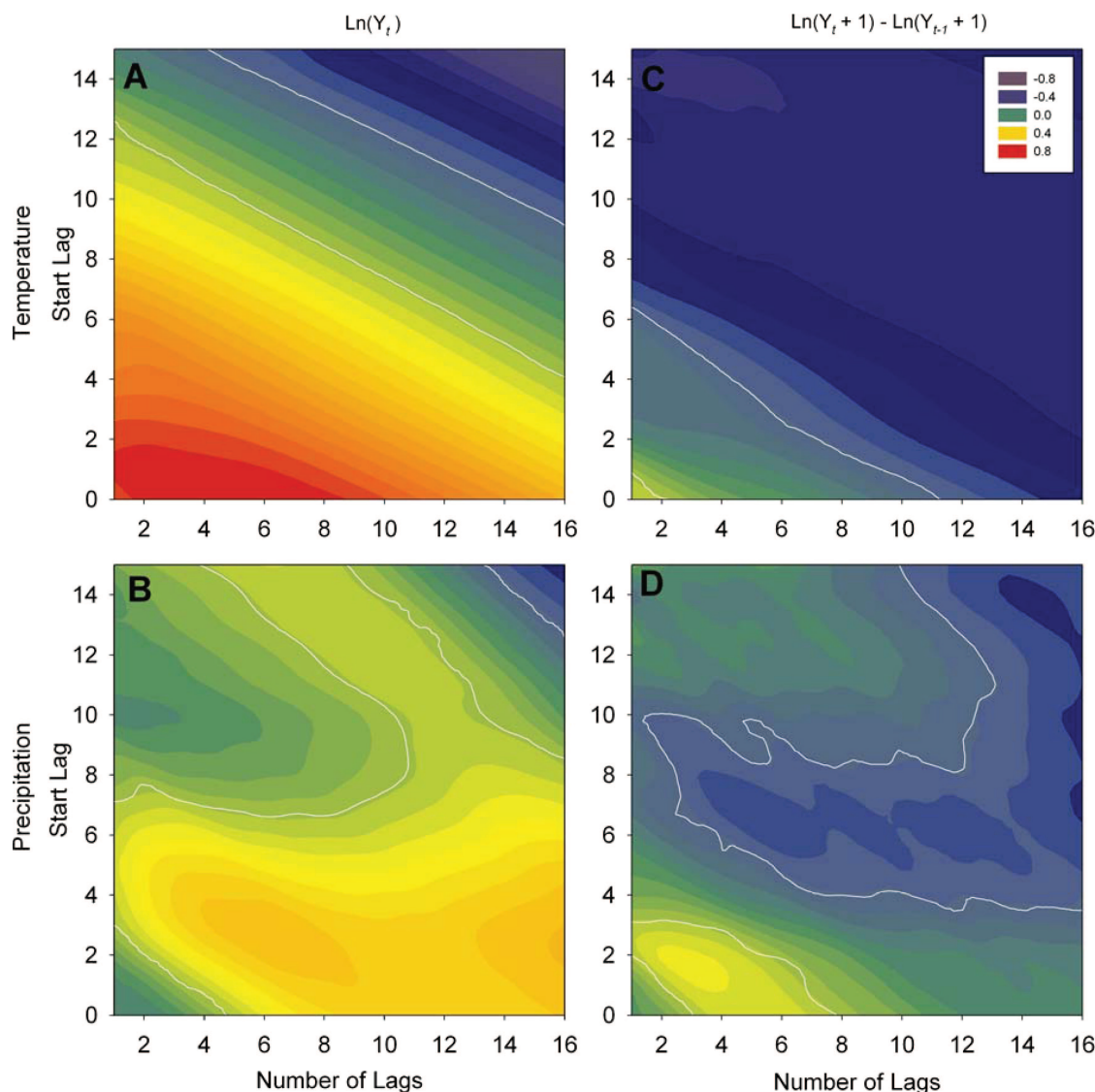
Fig. 2. Cross-correlation maps for mean collection per trap $(\ln(Y_t + 1))$ (A and B) and change in trap collections $\ln(Y_t + 1) - \ln(Y_{t-1} + 1)$ (C and D) with temperature and precipitation lagged 0–15 wk and duration of 1–15 wk before the initial lag. Starting lag is on the y-axis and number of subsequent lags summed with the starting lag is on the x-axis. White contours represent the 0.05 significance level. $n = 165$ (A and B) and 160 (C and D).

cated in the approximate center of the ARDC property. Mean daily, weekly, and monthly temperatures were based upon the daily high plus low divided by two and then averaged for the respective time period. Precipitation is given as mean weekly totals for the indicated periods. Degree-days (DD) were calculated from daily maximum − minimum temperatures by using sine-wave integration (Allen 1976) with a threshold of 10°C. Cumulative degree-days were calculated from the beginning of week 1 for each year.

Cross-correlation maps (Curriero et al. 2005) were used to explore the association between stable fly populations and climatic variables. Cross-correlation maps are similar to cross correlation plots with an

added dimension to examine the effects of event duration. Pearson Product Moment correlations between weekly mean trap collections and climatic variables 0–15 wk before collection were plotted on the y-axis. Zero to fifteen subsequent lags were averaged with the initial lag and plotted on the x-axis. Maps were produced from the correlation coefficient matrix by using the contour plot option in SigmaPlot (Systat Software, Inc., Point Richmond, CA), which uses the methods of Renka (1996) to interpolate three-dimensional surfaces. A significance level of 0.05 was used for all of the correlation analyses.

Stepwise multiple regression analyses, beginning with temperature (T), T^2, precipitation (p), p^2, pre-

Table 1. Covariate estimates for $\ln(Y_t + 1)$ model based upon temperature (T) and precipitation (p) with 49 mm/wk upper threshold

Covariate	F	Parameter $\pm$ SE	r^2
Model		df = 1, 161	0.78
$T_{t-(0:2)}$	132.34***	0.210 ± 0.018	0.63
T_{t-7}	8.18**	0.039 ± 0.014	0.03
$p_{t-(3:6)}$	31.70***	0.066 ± 0.012	0.11
Intercept		-1.256 ± 0.340	

**, $P < 0.01$; ***, $P < 0.001$.

Table 2. Covariate estimates for $\ln(Y_t + 1)$ model with $\ln(Y_{t-1} + 1)$ included as a covariate based upon temperature (T) and precipitation (p) with 49 mm/wk upper threshold

Covariate	F	Parameter $\pm$ SE	r^2
Model	254.41***	df = 3, 156	0.83
$\ln(Y_{t-1}+1)$	104.62***	0.506 ± 0.049	0.73
$T_{t-(0:1)}$	77.38***	0.112 ± 0.013	0.07
$p_{t-(3:6)}$	32.22***	0.050 ± 0.009	0.04
Intercept	11.04***	-0.627 ± 0.189	

**, $P < 0.01$; ***, $P < 0.001$.

cipitation truncated at 25 mm/wk (p_{25}) and p_{25}^2, were conducted using the PROC REG procedure (SAS Institute 2004). The stepwise selection method was used with 0.05 as the significance level for entry and 0.001 as the significance level for staying in the models. All climatic variables were included at week 0 and lagged up to 15 wk. Because the lagged variables are expected to be correlated, those included in the final model were combined into single terms by averaging. Combined terms and interaction terms for significant covariates were then added to the initial models, and stepwise regression was repeated. Once a final model was derived, the upper threshold on weekly precipitation was varied to maximize the F value of the model. The basic model was as follows:

$$Y_t = a + b_1 W_1 + b_2 W_2 \ldots$$

where Y_t is the fly population in week t, W_1, and W_2 are values for weather variables, and a and b are constants. For the autoregressive model, Y_{t-1} was included as a covariate.

The Durbin–Watson d statistic (Durbin and Watson 1951) was used to test for serial autocorrelation of the weekly trap collection data. Parameters for the covariates were rederived using PROC MIXED with the Repeated option and autoregressive covariance structure of the error matrix (SAS Institute 2004) when significant serial autocorrelation of the residuals was observed.

The effects of temperature and precipitation on annual variation in stable fly populations were examined by comparing the total numbers of flies collected in 4-wk periods beginning with weeks 17–20 with monthly temperature and precipitation data for the preceding nine 4-wk periods. Cross-correlation charts were used to identify correlation patterns.

Results

Generally, stable fly populations in eastern Nebraska were bimodal, characterized by high early and late summer populations (Fig. 1). Stable flies were collected during the first trapping period for 2001–2004 so the date of earliest activity could not be determined. In 2001, six stable flies (mean 1.0 per trap) were collected during the first trapping week with 71 DD_{10}; in 2002, five stable flies (mean 0.8 per trap) with 117 DD_{10}; in 2003, 92 (mean 3.7 per trap) stable flies with 260 DD_{10}, and in 2004, 30 stable flies (mean 1.2 per trap) with 145 DD_{10}. Traps were activated earlier

in 2005, 14 March, and no stable flies were collected until 29 March, one fly (mean 0.04 per trap) after 55 accumulated DD_{10}. For all years, consistent collections averaging more than one fly per trap began in mid-April after 133.4 ± 50.4 DD_{10} (mean $\pm$ SD; $n = 4$). Populations increased rapidly to >15 flies per trap each year in mid-May at 255.2 ± 31.1 DD_{10} ($n = 5$). Stable fly populations reached the early season peak in late June to early July at 715.0 ± 135.3 DD_{10} ($n = 5$). An anomalous midsummer peak was observed in early August of 2002. Most years, the early peak exceeded the late summer peak, but in 2003, the late summer peak was nearly twice as high as the early peak.

Cross-correlation maps indicated the greatest correlation of collection abundance occurred with mean weekly temperature lagged 0 wk with a duration of 1 to 8 wk (weeks 0–8 before collection week), and precipitation lagged 3 wk with a duration of 4 to 6 wk (Fig. 2A and B). Stepwise multiple regressions substantiated that the primary covariates were temperature lagged 0 to 2 wk and precipitation lagged 3 to 6 wk. Temperature lagged 7 wk was also significant. The resulting model was $\ln(Y_t + 1) = -1.511 + 0.196$ $T_{t-(0:2)} + 0.053$ $T_{t-7} + 0.089$ $p_{t-(3:6)}$ with an upper precipitation threshold of 49 mm/wk (Table 1; Fig. 1), where Y is number of stable flies per trap, t is current week, $T_{t-(x:y)}$ is mean daily temperature during the period starting x weeks before the collection week and ending y weeks before the collection week, and $p_{t-(x:y)}$ is mean weekly precipitation in millimeters per week during the x to y period. Analysis of residuals indicated that they were normally distributed with stable variance. However, the Durban–Watson (D-W) test indicated that the residuals exhibited a positive serial autocorrelation (D-W D = 1.16, $P < 0.0001$). Therefore, the model was reestimated using the PROC MIXED procedure. No consistent patterns of deviation between model predictions and observed collections were observed, either seasonally or annually, when residuals were plotted against time (weeks) or degree-days.

Cross-correlation maps examining the association between weekly stable fly population changes $\ln(Y_t + 1) - \ln(Y_{t-1} + 1)$ and climatic variables indicated lower correlation between climatic variables and population change than was observed between climatic variables and population levels. T_0 was positively correlated with population change, whereas temperature 7–15 wk before collection was negatively correlated with population changes ($P < 0.05$). Precipitation 2–8
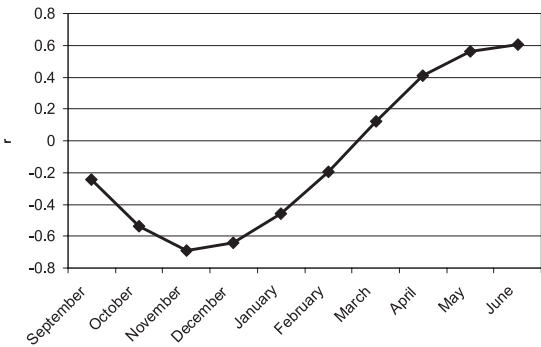
Fig. 3. Correlation of June stable fly population totals with mean temperature for 4-wk intervals before collection.

wk before collection was positively correlated with population change, whereas precipitation 6–10 wk prior was negatively correlated with population change (Fig. 2C and D). Inclusion of $\ln(Y_{t-1} + 1)$ as a covariate in the stepwise regression analysis resulted in $\ln(Y_t + 1) = -0.627 + 0.506 \ln(Y_{t-1} + 1) + 0.112$ $T_{t-(0:1)} + 0.050 \, p_{t-(3:6)}$ (Table 2). R^2 for the autoregressive model was 0.83. Residuals in this model were not serially autocorrelated (D-W D = 2.03, $P = 0.51$).

Total collections for weeks 25–28, which corresponded with the early summer peak, were correlated with mean monthly temperatures during the previous winter and spring (Fig. 3). The correlation was negative for the period coinciding with November–February and positive for April and May. Although significant correlations were observed between stable fly populations during other parts of the season with temperature or precipitation during the preceding 9 mo,

Table 3. Covariate estimates for $\ln(Y_t + 1)$ during midsummer season (weeks 24–40) (precipitation upper threshold 50 mm/wk)

Covariate	F	Parameter ± SE	r^2
Model		df = 1, 77	0.34
$T^2_{t-(0:2)}$	13.31***	0.153 ± 0.042	0.17
$p_{t-(3:5)}$	14.24***	0.048 ± 0.013	0.16
Intercept		1.000 ± 0.988	

***, $P < 0.001$.

none exhibited patterns that indicated biological meaning.

Overlaying seasonal population profiles with precipitation $p_{t-(3:6)}$ (Fig. 4) illustrates the association between the lower stable fly populations observed in midsummer and reduced precipitation during the previous 3–6 wk. Stepwise multiple regression of stable fly populations between the early and late season population peaks, weeks 24–40, found temperature 0–2 wk before collection and precipitation 3–5 wk before collection to be significant with positive estimates (Table 3).

Discussion

Overall patterns of stable fly populations during the 5 yr of this study were similar to those observed by others in the Central Plains region (Black and Krafsur 1985, Scholl 1986, Guo et al. 1998, Broce et al. 2005). The 55 DD_{10} accumulated before the appearance of the first fly collections would not be adequate for a complete generation; hence, these flies must have either overwintered or immigrated (Broce et al. 2005). Assuming a generation time of 258 DD_{10} (Lysyk 1993)
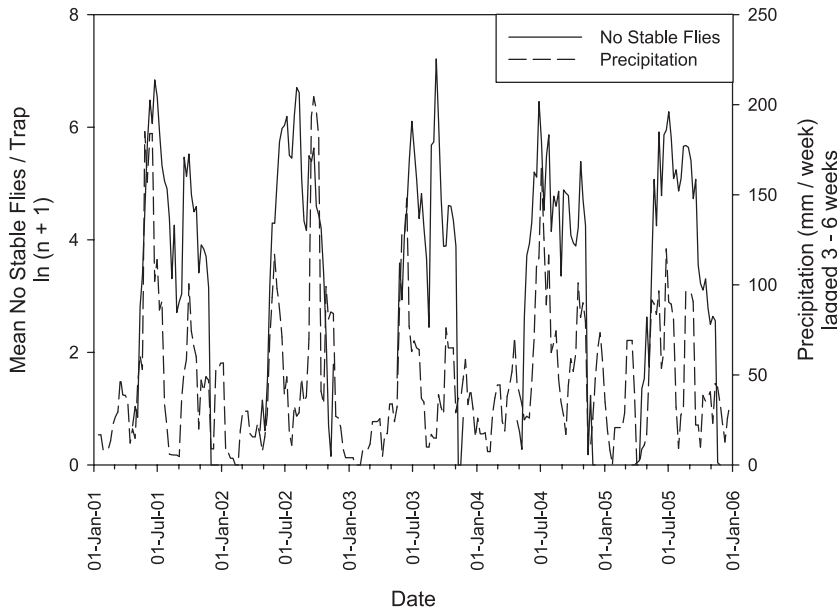

Fig. 4. Comparison of mean weekly precipitation 3–6 wk earlier ($p_{t-(3:6)}$) with seasonal stable fly trap collections ($p_{t-(3:6)}$ is the running mean of weekly precipitation totals for the period 3–6 wk before the collection date).

and appearance of initial flies, either immigrant or overwintering, at 55–150 DD_{10}, the June–July peak stable fly population would represent the F_2 progeny of the initial flies. The primary source of stable flies in the early summer population seems to be sites where large round bales are fed to cattle during the winter. Broce et al. (2005) made this observation in Kansas, and we also have observed it in eastern Nebraska. According to Broce et al. (2005), larval production in the round bale-feeding sites diminishes in midsummer due to increasing temperatures and lower rainfall. Our analysis indicates that reduced fly populations in mid-summer are associated with lower rainfall 3 to 6 wk earlier, but higher temperatures do not seem to be a factor. Indeed, populations during the decline remain positively correlated with temperature rather than negatively as would be expected if high temperatures were a factor. Late summer stable fly populations are more variable than early summer populations. The early summer peak was consistently the last week of June or first week of July each of the 5 yr. However, the late summer peak occurred between mid-August and mid-October.

Our findings of the importance of precipitation on stable fly populations are similar to those of Mullens and Peterson (2005), but differ from those of Lysyk (1993), who failed to find a relationship between precipitation and stable fly population levels. Stable flies require ≈13 d for larval development at 25°C (Gilles et al. 2005), and Alsynite traps catch primarily young flies, 0–2 d old (Guo et al. 1998). Precipitation 3 to 6 wk before collection as adults would indicate that the larval habitat must be moist for oviposition to occur. This is supported by Romero et al. (2006) who found that female flies are attracted and oviposit in response to bacterially derived stimuli. Once thoroughly wetted, the highly organic media is capable of remaining moist in the absence of rain through the 2 wk required for larval development. Precipitation in excess of 50 mm per week supported no significant added increase in stable fly population levels. However, there was no indication that excess precipitation was deleterious.

Temperature and precipitation account for most of the variation observed in stable fly populations, both within and between years. The addition of the autoregressive covariate $\ln(Y_{t-1} + 1)$ to the model increased the R^2 value by only 0.04. The temperature 7 wk before collection (T_{t-7}) term included in the nonautoregressive model seems to account for the population level in the previous generation adding an autoregressive component to that model. T_{t-7} and Y_{t-1} were correlated ($r = 0.584$). T_{t-7} was not significant in the autoregressive model.

Stable flies are highly adaptable, exploiting many different habitats for larval development depending upon the cultural practices in different regions. Large numbers of stable flies are produced in association with confined cattle (Meyer and Petersen 1983). They are also pest of pasture animals, and they have been associated with winter hay feeding sites (Broce et al. 2005). In many parts of North America, cattle are either not fed hay during the winter, or large round bale feeders are not used. The relationship between stable fly populations and climatic variables may vary depending upon the larval developmental sites used. In addition, high temperatures may be more of a factor in limiting stable fly populations in warmer regions. These models need to be verified in regions with different cultural and climatic conditions to determine their universality.

Our results predict that peak stable fly abundance will be greater in years following prolonged, cold winters and warm springs. Within years, densities are greater when antecedent weather was warmer and wetter. Under the conditions observed in eastern Nebraska, precipitation, not temperature, seems to be the primary factor limiting stable fly populations in midsummer.

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